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Research

Phylogenetic conservatism and biogeographic affinity influence woody plant species richness–climate relationships in eastern Eurasia

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Mechanisms underlying species richness patterns remain a central yet controversial issue in biology. Climate has been regarded as a major determinant of species richness. However, the relative influences of different evolutionary processes, (i.e. niche conservatism, diversification rate and time for speciation) on species richness–climate relationships remain to be tested. Here, using newly compiled distribution maps for 11 422 woody plant species in eastern Eurasia, we estimated species richness patterns for all species and for families with tropical and temperate affinities separately, and explored the phylogenetic signals in species richness patterns of different families and their relationships with contemporary climate and climate change since the Last Glacial Maximum (LGM). We further compared the effects of niche conservatism (represented by contemporary-ancestral climatic niches differences), diversification rate and time for speciation (represented by family age) on variation in the slopes of species richness–climate relationships. We found that winter coldness was the best predictor for species richness patterns of most tropical families while Quaternary climate change was the best predictor for those of most temperate families. Species richness patterns of closely-related families were more similar than those of distantly-related families within eudicots, and significant phylogenetic signals characterized the slopes of species richness–climate relationships across all angiosperm families. Contemporary-ancestral climatic niche differences dominated variation in the relationships between family-level species richness and most climate variables. Our results indicate significant phylogenetic conservatism in family-level species richness patterns and their relationships with contemporary climate within eudicots. These findings shed light on the mechanisms underlying large-scale species richness patterns and suggest that ancestral climatic niche may influence the evolution of species richness–climate relationships in plants through niche conservatism.

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Introduction

Understanding the latitudinal gradient in species richness (i.e. the decrease in species richness with latitude) has been a central question in biology for two centuries, and yet it remains a major challenge to biologists (Hawkins 2001). Although many authors have explored the influences of contemporary climate (Francis and Currie 2003, Hawkins et al. 2003a), historical climate change (Svenning and Skov 2007, Araújo et al. 2008) and habitat heterogeneity (Kerr and Packer 1997, Stein et al. 2014) on species richness patterns, the evolution of these relationships has not been fully understood (Ricklefs 2006). With the increasing availability of phylogenetic data, an integrative framework incorporating ecological and evolutionary processes has been suggested for understanding the evolution of species richness–environment (especially climate) relationships (Ricklefs 2006).

To understand the evolutionary mechanisms of species richness patterns, several hypotheses have been proposed in previous studies, including the niche conservatism hypothesis, diversification rate hypothesis and time-for-speciation hypothesis. Niche conservatism, i.e. the tendency of species to retain their ancestral niches (Wiens and Graham 2005), has been regarded as an important mechanism to explain the latitudinal gradients in species richness (Latham and Ricklefs 1993a, b, Ricklefs et al. 1999, Wiens and Donoghue 2004, Wiens et al. 2010). The niche conservatism hypothesis suggests that 1) conservatism in species' niches leads to similar climatic adaptations among closely-related species/clades and constrains them to inhabit similar climates which are close to their ancestral niches (Wiens and Donoghue 2004, Davis 2005, Hof et al. 2010, Giehl and Jarenkow 2012); and 2) the constraints on species richness induced by climate tend to be strengthened when climate deviates from its ancestral climate (Xu et al. 2013, 2019b). As a result, niche conservatism likely leads to more similar species richness patterns and species richness–climate relationships among more closely related clades (Ricklefs 2006), and leads to lower species richness and flatter species richness–climate relationships of clades with larger differences between ancestral and contemporary climatic niches. However, both predictions of niche conservatism hypothesis remain to be fully understood. Moreover, evolutionary affinities of clades could also influence their species richness–climate relationships through niche conservatism (Harrison and Grace 2007, Wang et al. 2011). Specifically, clades with tropical affinities might be prevented from colonizing temperate zones due to lack of cold adaptations (Wiens et al. 2006, Wang et al. 2011), and hence winter coldness has been found to be the dominant factor for their species richness patterns (Latham and Ricklefs 1993b,

Wang et al. 2011). In contrast, clades with temperate affinity are adapted to cool climate and hence may not be strongly limited by winter coldness (Wang et al. 2011, Shrestha et al. 2018). Most studies testing the effect of niche conservatism on species richness–climate relationships are usually based on tetrapods (Hawkins et al. 2006, Weir and Schluter 2007, Buckley et al. 2010, Pyron and Wiens 2013, Duchêne and Cardillo 2015) but rarely for plants (but see Kerkhoff et al. 2014, Folk et al. 2019).

The diversification rate hypothesis posits that high species richness in some regions are due to high diversification rate caused by high speciation rate and/or low extinction rate (Mittelbach et al. 2007). For example, previous studies have indicated that high diversification rate in ancestral climates of several plant groups might be the dominant driver for their species richness patterns (Svenning et al. 2008a, Wang et al. 2018). In contrast, the time-for-speciation hypothesis suggests that regions that have been colonized longer and hence have experienced more time for species to accumulate through speciation tend to have higher species richness (Stephens and Wiens 2003). This hypothesis has been used to explain higher species richness in ancestral climates than others due to longer time for in situ diversification for several clades of plants and tetrapods (Latham and Ricklefs 1993b, Smith et al. 2005, Wiens et al. 2006, Pyron and Burbrink 2009). Diversification rates within clades have been found to be positively associated with within-clade niche divergence and rates of climate-niche evolution (Kozak and Wiens 2010b, Keller and Seehausen 2012), and hence rapid diversification and niche conservatism may represent opposing directions of clade evolution (Ackerly 2009). Moreover, clades originating in different time (i.e. different ages) may have different ancestral climate due to paleo-climate fluctuations during geological histories (Royer et al. 2004, Buckley et al. 2010). These findings suggest that in addition to their effects on species richness patterns, diversification rate and time for speciation may also influence species richness–climate relationships (Ricklefs 2006, Buckley et al. 2010, Kozak and Wiens 2010b). However, whether clades with different diversification rates and evolutionary time have different species richness–climate relationships remains to be tested.

Studies have indicated that severe glacial–interglacial climate fluctuations since the Quaternary might also have influenced large-scale patterns of species richness (Dynesius and Jansson 2000). Because temperate and boreal regions, where clades with temperate affinity are assumed to have originated, were strongly affected by glaciation during the Last Glacial Maximum (Sandel et al. 2011), a large portion of habitats for temperate clades may have been covered by glaciers during this period. The distribution of temperate clades may, thus, have been constrained more by the past climate change as compared to clades with tropical affinity. Evidence for the importance of past climate change in shaping patterns of species richness has been found for reptiles and amphibians in Europe (Araújo et al. 2008), mammals and birds in North America (Hawkins and Porter 2003), and Holarctic trees

(Montoya et al. 2007). However, the relative importance of past climate change on clades with different evolutionary affinities (e.g. tropical versus temperate) is yet to be explored.

Here, using a newly compiled distribution database for 11 422 woody plant species in eastern Eurasia (see methods for details on its definition), we illustrated the influence of three evolutionary processes (namely niche conservatism, diversification rate and time for speciation) on species richness–climate relationships across woody plants families with tropical- and temperate-affinities. Specifically, we aim to test the following hypotheses. 1) The dominant environmental factors for species richness patterns differ between families with tropical and temperate affinities. 2) Closely-related families have more similar species richness patterns and species richness–climate relationships than distantly-related families. 3) Among the three evolutionary processes, niche conservatism dominates the variations in species richness–climate relationships across families through the magnitudes in the differences between ancestral and contemporary climatic niches.

Material and methods

Study area

We defined eastern Eurasia as the area to the east of 90°E longitude encompassing China, Mongolia and part of Russia. We excluded the regions to the west of 90°E longitude because most of northwestern China and central Asia are drylands and only have a small number of woody plants. Because we lack high resolution species distribution data for continental southeast Asia (i.e. the Indochina Peninsula) and the Korean Peninsula, we also excluded these regions to eliminate possible bias in species richness estimation. The territory of eastern Eurasia defined herein covers a latitudinal gradient of > 57°, ranging from ca 20°N to ca 77°N latitude and encompasses a broad gradient of climate and vegetation types. Specifically, eastern Eurasia has a continuous spectrum of forest vegetation ranging from tropical rainforests through subtropical evergreen forests and temperate deciduous forests to boreal forests. This area also has diverse non-forest vegetation including alpine and temperate steppes, meadows and deserts. In comparison to continental North America and Europe, eastern Eurasia harbors more woody plant species, especially relict and endemic ones (Latham and Ricklefs 1993a, Qian and Ricklefs 2000). Therefore, eastern Eurasia is suitable for studying large-scale patterns of species richness and their drivers.

Species distribution data and biogeographical affinities

The distributions of woody plants in eastern Eurasia were compiled from published atlases of woody plants and online databases of the three countries in this area (i.e. China, Mongolia and Russia). Distribution data from China were

mainly compiled from the ‘Atlas of woody plants in China: distribution and climate’ (Fang et al. 2011, Wang et al. 2011) and updated with new records from the National Specimen Information Infrastructure (<www.nsii.org.cn/>, accessed in July 2015). The distribution data for Mongolia were compiled from the ‘Virtual guide to the flora of Mongolia’ (<<http://greif.uni-greifswald.de/floragreif/>>), ‘Conspectus of the vascular plants of Mongolia’ (Urgamal et al. 2014) and ‘Rangeland plants of Mongolia’ (Undarmaa et al. 2015). Distributional data from Russia were compiled from ‘Woody plants of the Asian part of Russia’ (Koropachinskiĭ et al. 2002) and ‘The distribution of trees and shrubs in USSR’ (Ареалы деревьев и кустарников СССР, 3 volumes, in Russian), which provide distribution maps of all woody plant species in Russia and the former Soviet Union.

Species names from different data sources were standardized following ‘The catalogue of life’ (<www.catalogueoflife.org/>) and ‘The Plant List database’ (<www.theplantlist.org/>, accessed 12 March 2014). The former database is generated by Species 2000 and the Integrated Taxonomic Information System (ITIS), and the latter is a working list of all known vascular plants and bryophytes, which provides the accepted Latin names and synonyms for most plant species. The family names of angiosperm woody plants were adjusted following the Angiosperm Phylogeny Website (<www.mobot.org/MOBOT/research/APweb/>). Records referring to cultivated and/or introduced species were removed from the database. The final database included 11 422 species belonging to 156 families. Woody plant species were defined as perennial species with a persistent aboveground stem and ligneous materials (Zanne et al. 2014, Bettenfeld et al. 2020), and are normally either trees, shrubs or lianas.

The species distribution data from the three countries were digitized and rasterized at a spatial resolution of 100 × 100 km. Species richness in each grid cell was estimated as the number of species occurring in it. To eliminate the effects of area on species richness estimation, incomplete grid cells located along country borders or coastal areas (with less than half of their area being on land) were excluded. In the final analyses, 1856 grid cells were included.

To compare the effects of environmental variables on patterns of species richness with different biogeographic affinities, we used the framework of Wu et al. (2006), which categorizes terrestrial families into tropical, temperate and cosmopolitan affinities based on the fossil and contemporary distributions of each family at the global scale, the evolutionary history of each family, and the relationships between the floras of major biogeographic regions (Wu 1991, Wu et al. 2003, 2006). This classification scheme of family affinities has been widely used in previous studies exploring plant richness patterns (Qian et al. 2003, Wang et al. 2011). In our analyses, 87 families containing 5135 woody plant species were classified as tropical affinity, 38 families containing 2226 woody plant species as temperate affinity, 28 families containing 4044 woody plant species as cosmopolitan affinity and three families containing 17 woody plant species as

unknown affinity (see Supplementary material Appendix 1 for the family list in eastern Eurasia).

We also compiled global species distributions of angiosperm species from published floras, checklists, online databases and peer-reviewed papers (see Supplementary material Appendix 2 for the complete list of data sources) at a spatial resolution of ca 150 000 km² (ca 4 longitude × 4 latitude). The same data compilation method and the boundaries of the geographical units were used in recent studies (Xu et al. 2013, Shrestha et al. 2018, Wang et al. 2018, Xu et al. 2019b) for different plant groups. These data were used to estimate the global distribution and contemporary climatic niche of each family.

Environmental variables

To evaluate the effects of contemporary climate on species richness patterns, six variables were used, including mean annual temperature (MAT), mean temperature of coldest quarter (MTCQ), mean annual precipitation (MAP), annual evapotranspiration (AET), temperature annual range (ART) and precipitation seasonality (PSN). These variables were categorized into three groups: environmental energy (MAT, MTCQ), water availability (MAP, AET) and climate variability (ART, PSN). Data for MAT, MTCQ, MAP, ART and PSN with spatial resolution of 2.5 arc minutes were obtained from the WorldClim website (Hijmans et al. 2005). AET with a resolution of 30 arc-seconds was obtained from the CGIAR Consortium for Spatial Information (<www.cgiar-csi.org/>). AET reflects the amount of water that plants could actually use, and is often used as a surrogate of net primary productivity (NPP) (Hawkins et al. 2003b).

To evaluate the effects of habitat heterogeneity on species richness, we used elevation range (RELE) and number of vegetation types (VEGE) within each grid cell. RELE was calculated as the difference between the maximum and minimum elevation within a grid cell and has been used as a surrogate of topographic complexity in previous studies (Kerr and Packer 1997). The topography data were obtained from the WorldClim website (<<http://worldclim.org/>>) (Hijmans et al. 2005) at the spatial resolution of 30 arc-seconds. VEGE was used to represent vegetation heterogeneity (Wang et al. 2012a), and was estimated from global land cover characteristics data obtained from the USGS (<www.usgs.gov/>) at the spatial resolution of 1 km. These two variables did not exhibit normal distributions, and hence were log-transformed prior to analyses.

To evaluate the effects of long-term climate changes since the Last Glacial Maximum (LGM, ca 18 000–22 000 yr. BP) on species richness, we estimated MAT anomaly (MAT_{ano}) and MAP anomaly (MAP_{ano}) since the LGM for each grid cell (Araújo et al. 2008). MAT_{ano} was calculated as the difference in MAT between the LGM and the present (i.e. MAT_{present} – MAT_{LGM}) and was used to represent the change in mean annual temperature since the LGM. Similarly, MAP_{ano} was estimated as the difference in MAP between the LGM and the present.

Data on LGM temperature and precipitation with spatial resolutions of 2.5 arc minutes were downloaded from the WorldClim website (<<http://worldclim.org/>>), which were statistically downscaled from original output of general circulation models (GCMs) (Hijmans et al. 2005). Two GCMs have been widely used in previous studies to evaluate the effects of LGM climate on species distributions in eastern Eurasia (Worth et al. 2013, Kimura et al. 2014, Tsuyama et al. 2014): the Model for Interdisciplinary Research on Climate (MIROC-ESM) (Watanabe et al. 2011) and the Community Climate System Model (CCSM) (v3 and v4) (Collins and Halliday 2005, Gent et al. 2011). We used the data reconstructed by MIROC-ESM (Watanabe et al. 2011) in our study because comparison of the effects of these two GCMs on vegetation distributions in eastern Eurasia suggests that MIROC-ESM is more realistic than CCSM (Worth et al. 2013, Kimura et al. 2014, Tsuyama et al. 2014).

The average values for each environmental variable within each grid cell were estimated with the zonal statistics tool in ArcGIS 10.0. Pearson correlations among all environmental variables were calculated to check for multicollinearity (Supplementary material Appendix 3 Table A3.1).

Effects of environment on species richness patterns

We evaluated the effects of all environmental variables (see above) on the species richness of each family separately. Here, we only chose families with at least five species because this number represented the lowest quartile of species richness of all families. We repeated the analyses with a threshold of ten species and found consistent results for all analyses (Supplementary material Appendix 4). To make the regression slopes comparable between environmental variables for each family, we used the R function ‘scale’ to standardize all environmental variables as $(x_i - x_{\text{mean}})/x_{\text{sd}}$, where x_i is the value of the variable in the i th grid, and x_{mean} and x_{sd} are the mean and standard deviation of that variable across all grid cells.

Because species richness normally fits a Poisson distribution (Wang et al. 2011), generalized linear models (GLMs) with quasi-Poisson errors and log link function were used to evaluate the effects of environmental variables on species richness. In general, GLM with quasi-Poisson errors could compensate for the over-dispersion in data compared with GLM with Poisson errors (Crawley 2007). As spatial autocorrelation in species richness patterns may inflate type I errors in significance tests of regression models, we used the adjusted R^2 (R^2_{adj}) of models instead of p values to evaluate model performance. R^2_{adj} (%) was estimated as $100 - 100 \times (\text{residual deviance}/\text{residual DF})/(\text{null deviance}/\text{null DF})$ (Faraway 2016). Using the R^2 of each environmental variable on the species richness pattern of each family, we identified the dominant factor for each family (i.e. the environmental factor with the highest R^2), and then counted the number of families that were primarily dominated by each environmental factor. We compared the average R^2 of different environmental factors on family-level species richness patterns using the Tukey honest significant difference method (TukeyHSD) for all families

and families with tropical and temperate affinities respectively. We also extracted the standardized regression coefficients (i.e. the slopes) of the species richness–climate relationships for all families for the following analyses.

Phylogenetic signals in species richness patterns and their relationships with climate

Three dated angiosperm phylogenies reconstructed by Magallón et al. (2015), Harris and Davies (2016) and Barba-Montoya et al. (2018) were compiled. These phylogenies provide the relationships and divergence time between angiosperm families and have been widely used in previous studies (Huang et al. 2015, Gómez et al. 2019, Xu et al. 2019a).

We conducted three calculations to evaluate the effects of phylogenetic relatedness on the similarities between patterns of species richness of different families. First, we calculated the cell-wise Pearson correlation coefficients between the species richness patterns for each pair of families (r_{fa}). We excluded grid cells where species richness of either families was zero as zero-inflation could bias estimates of regression models (Heilbron 1994, Blasco-Moreno et al. 2019). Second, we calculated the phylogenetic distances between each pair of families (D_{fa}) using the three family-level phylogenies separately. To test the significance of the relationship between r_{fa} and D_{fa} , we built a null model by randomizing the tips of each phylogeny 1000 times and recalculating D_{fa} (denoted as D_{fa}') and slopes between r_{fa} and D_{fa}' . We then used the Wilcoxon rank-sum test to compare the observed $r_{fa} - D_{fa}$ slopes with $r_{fa} - D_{fa}'$ slopes based on 1000 randomizations. Third, we binned D_{fa} into seven groups with equal intervals (i.e. 50 Myr) starting from 150 Ma, and then calculated the mean r_{fa} and the proportions of weak ($r_{fa} < 0.3$, 0.2 or 0.1) and negative r_{fa} within each group.

Blomberg's K (Blomberg et al. 2003) was used to evaluate phylogenetic signals in climatic niches and the slopes (standardized regression coefficients) of species richness–climate relationships of different families. The contemporary climatic niche of each family was estimated as the average of each climate variable within its distribution range weighted by species richness per grid cell. Blomberg's K values significantly higher than 0 indicate significant phylogenetic signals in niche evolution, with higher K values indicating stronger phylogenetic signals (Blomberg et al. 2003). $K=1$ indicates that niche evolution follows Brownian motion (Blomberg et al. 2003). Blomberg's K values were calculated using the R package 'phytools' (Revell 2012).

All above analyses were repeated using the three family-level phylogenies, which led to consistent results. We presented the results based on the one of Barba-Montoya et al. (2018) in the main text, and others in Supplementary material Appendix 3–4. Among angiosperm clades, the eudicot clade is the dominant one and contains 88 out of the 101 angiosperm families included in our study. Moreover, preliminary analyses suggested that the phylogenetic signals in niches of eudicot families were stronger than those for angiosperm families. Therefore, we repeated these analyses

for angiosperms and eudicots separately. We did not perform similar analyses for the remaining four angiosperm clades separately because the number of families with woody plant species in these clades was low.

Effects of niche conservatism, diversification rate and time for speciation on species richness–climate relationships

To test the effects of niche conservatism on species richness–climate relationships, we first reconstructed the ancestral climatic niches of all families using residual maximum likelihood (REML) method, a Brownian-motion based estimator, which is conducted with the 'ace' function in the R package ape (Paradis et al. 2004). We then estimated the absolute differences between the mean climate of each family in eastern Eurasia and its ancestral climatic niche (NC_{diff}). The ancestral climatic niche of a family was estimated as the reconstructed climate at the stem node or at the crown node. These two measures of ancestral climatic niches generated highly consistent results and those based on the first measure are presented in the main text and the others in the Supporting Information (Supplementary material Appendix 3–4).

To test the effect of diversification rate on species richness–climate relationships, we employed the method developed by Magallon and Sanderson (2001) to calculate the diversification rate of each family using its global species richness (which was compiled from the Catalogue of Life, <www.catalogueoflife.org/>) and stem age extracted from the three dated phylogenies. Following previous studies (Magallon and Sanderson 2001, Harris and Davies 2016), we considered two levels of extinction (i.e. no extinction, $\epsilon=0.0$; high extinction, $\epsilon=0.9$) in diversification rate estimations, which generated consistent results on the relationships between diversification rates and slopes of species richness–climate relationships. The results based on diversification rate estimation with low extinction were presented in the main text and others in the Supporting Information (Supplementary material Appendix 3–4). The stem age of each family was used as a proxy to test the effects of time for speciation on species richness–climate relationships.

To compare the effects of these three evolutionary processes, we conducted phylogenetic generalized least squares (PGLS) regression (Martins and Hansen 1997) with the R package 'caper' (Orme et al. 2018) using lambda maximum likelihood approach to transform branch lengths.

All analyses were conducted in R v3.3 (<<https://cran.r-project.org/>>).

Results

Species richness patterns in eastern Eurasia

Species richness in eastern Eurasia was high in southern and southwestern China and decreased with latitude (Fig. 1). The species richness of all families combined, and of families with

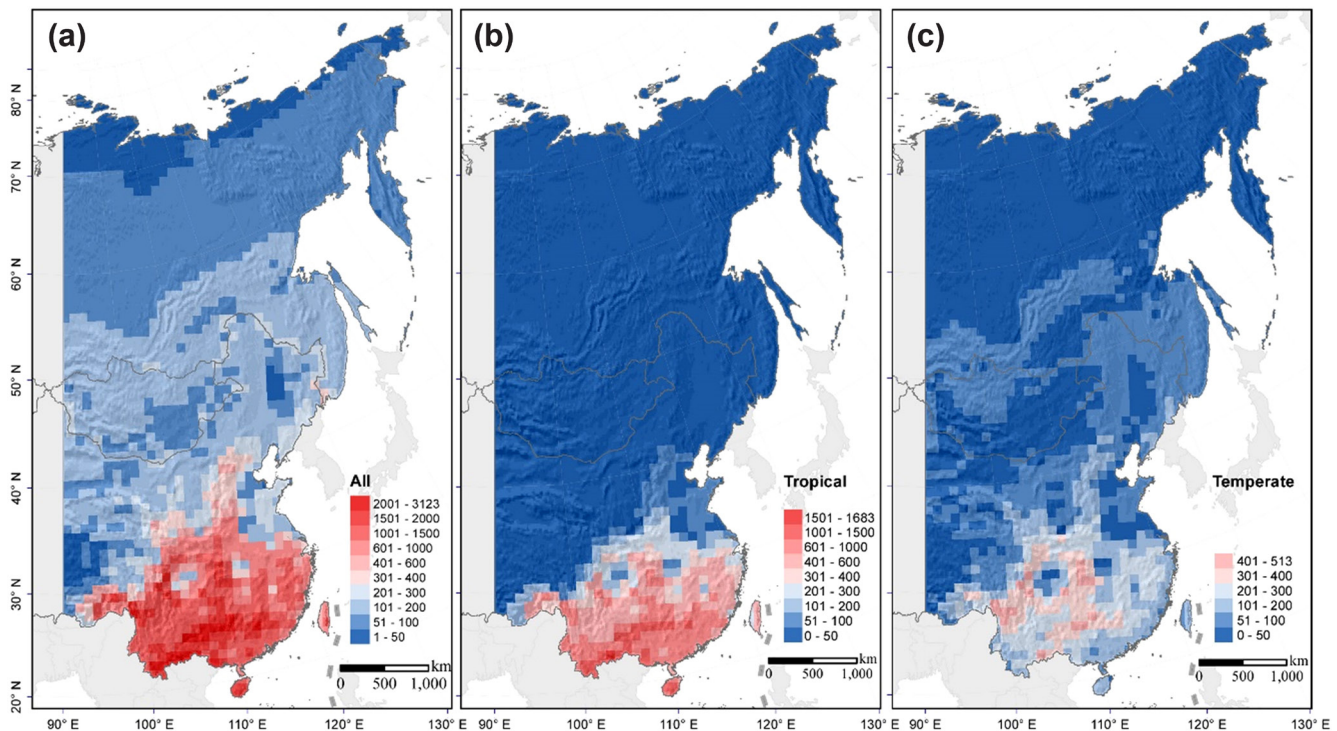


Figure 1. Species richness patterns for: (a) all woody plants, (b) families with tropical affinity and (c) families with temperate affinity.

tropical affinity, increased towards the tropical region, while that of temperate families was highest in subtropical regions at ca 30°N and then decreased towards both high and low latitudes. Species richness was associated with topography (Fig. 1), and was particularly high in mountainous areas (e.g. the hilly southern China, the Hengduan Mountains, the Qinling Mountains and the Xing'an Mountains), but low in lowlands (e.g. the Northeast Plain in China), plateaus (e.g. the Qinghai-Tibetan Plateau) and basins (e.g. the Sichuan Basin).

Environmental determinants of species richness patterns

The associations of species richness to climate differ between families with tropical and temperate affinities (Fig. 2–3; Supplementary material Appendix 3 Fig. A3.1–A3.6 and Supplementary material Appendix 4 Fig. A4.1–A4.2). Our results indicated that species richness of most tropical families was dominated by winter coldness (MTCQ), while that of most temperate families was dominated by temperature anomaly since the LGM (MATano) rather than by winter coldness. Specifically, when a cutoff of 5 (or 10) species was used, winter coldness had the highest explanatory power for species richness of 32 (or 26) tropical families, while temperature anomaly had the highest explanatory power for only 2 (or 2) tropical families. However, an inverse pattern was found for temperate families. Specifically, temperature anomaly had the highest explanatory power for 9 (or 7) temperate families, while winter coldness had the highest explanatory power for only 3 (or 2). In addition,

the average explanatory power of winter coldness on species richness was significantly larger than that of temperature anomaly for tropical families ($p < 0.05$ in the TukeyHSD test), but not for temperate families.

Phylogenetic signals in species richness patterns and their relationships with climate

The Pearson correlation coefficients between species richness patterns of different families (r_{fa}) for all angiosperms were negatively but not significantly correlated with the phylogenetic distance of corresponding family pairs (D_{fa}) (Fig. 4a–b; Supplementary material Appendix 3 Fig. A3.7–A3.8 and Supplementary material Appendix 4 Fig. A4.3–A4.5). However, for eudicot families, the negative relationship was significant (Wilcoxon rank-sum test, $p < 0.05$) (Fig. 4a, c; Supplementary material Appendix 3 Fig. A3.7–A3.8 and Supplementary material Appendix 4 Fig. A4.3–A4.5). With the increase in D_{fa} , the mean values of r_{fa} decreased and the proportions of family pairs with weak and negative r_{fa} increased for eudicots based on all phylogenies and for angiosperms based on the phylogenies of Magallón et al. (2015) and Harris and Davies (2016) (Supplementary material Appendix 3–4 Fig. A3.10–A3.11; Fig. A4.7–A4.8). When the phylogeny of Barba-Montoya et al. (2018) was used, these trends for angiosperms were only consistent with those of eudicots when $D_{fa} < 300$ Ma, but not when $D_{fa} > 300$ Ma, which may be due to the very old divergences in the Barba-Montoya et al. (2018) phylogeny and the very large phylogenetic distances between the basal

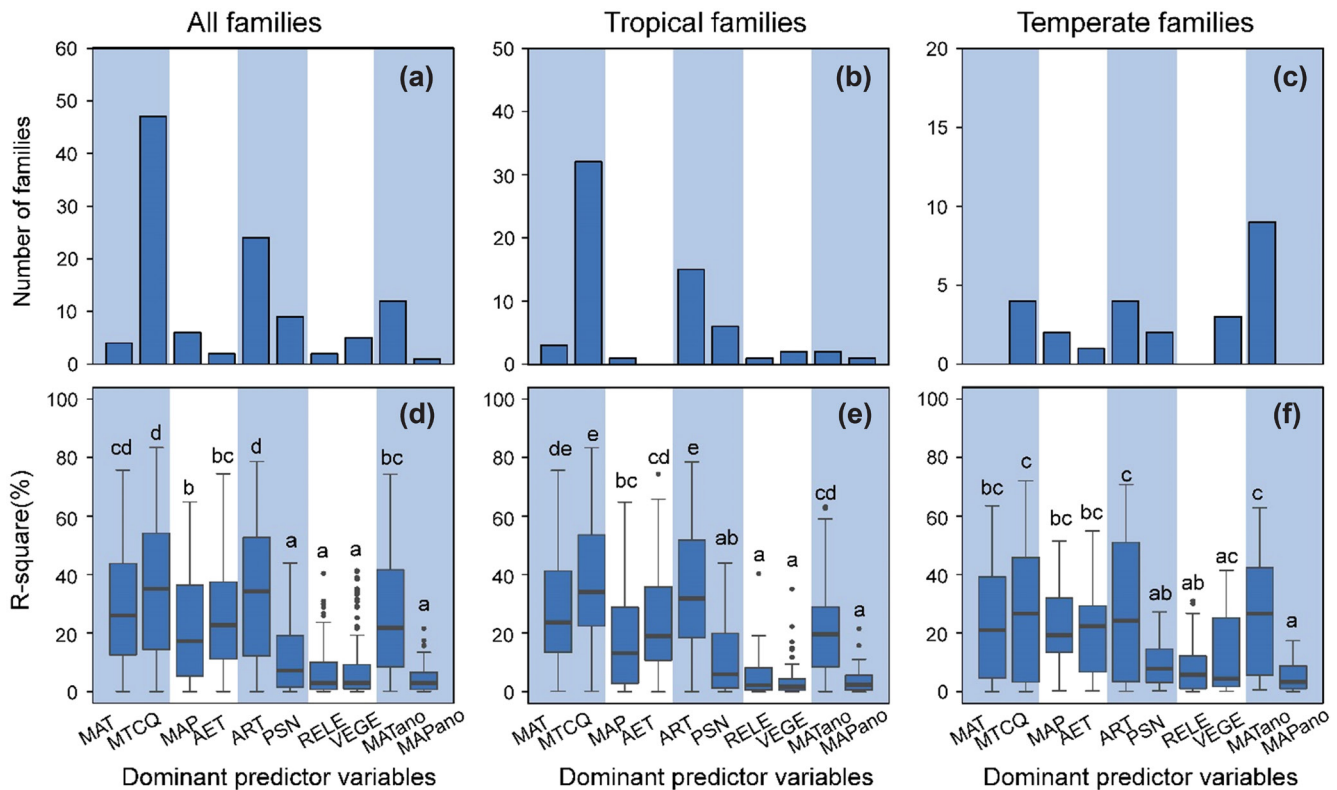


Figure 2. The number of families for which species richness was dominated by each environmental factor and the average R^2 of each environmental factor. (a, d) all woody plants, (b, e) families with tropical affinity and (c, f) families with temperate affinity. Species richness of most tropical families was dominated by winter coldness (MTCQ), while that of most temperate families was dominated by MAT anomaly (MATano). Mean R^2 of MTCQ was significantly higher than that of MATano for tropical families ($p < 0.05$), but not for temperate families. MAT: mean annual temperature, MTCQ: mean temperature of coldest quarter, MAP: mean annual precipitation, AET: annual evapotranspiration, ART: temperature annual range, PSN: precipitation seasonality, RELE: elevation range, VEGE: the number of vegetation type, MATano: mean annual temperature anomaly, MAPano: mean annual precipitation anomaly.

(i.e. Austrobaileyales and Chloranthales) and other angiosperm clades (Supplementary material Appendix 3–4 Fig. A3.9, A4.6). These results indicate that closely related families within eudicots tend to have similar species richness patterns, and that different hypotheses about the crown age of angiosperms may influence the estimation of phylogenetic signals in species richness patterns.

The phylogenetic signals in climatic niches evaluated by MAT, MTCQ, MAP, AET, ART and MATano were significant, and were stronger in eudicots than in angiosperms (Supplementary material Appendix 3–4 Table A3.2, A4.1). In contrast, PSN and MAPano had no phylogenetic signals in both angiosperms and eudicots.

The phylogenetic signals in the slopes of species richness–climate relationships were significant or marginally significant in most cases, and were stronger for eudicots than for angiosperms (Table 1; Supplementary material Appendix 3–4 Table A3.3, A4.2). Specifically, for all angiosperms the phylogenetic signals were significant for the slopes of richness–MTCQ and richness–MAP relationships, and marginally significant for the slope of richness–AET relationship. For eudicots, the phylogenetic signals were significant for the slopes of richness–MTCQ, –MAP, –AET and –ART

relationships. For both angiosperms and eudicots, the phylogenetic signals were the strongest for the slopes of richness–MTCQ and richness–MAP relationships among all richness–climate relationships.

Effects of niche conservatism, diversification rate and time for speciation on species richness–climate relationships

The difference between ancestral and contemporary climatic niches of families (NC_{diff}) were the strongest predictor of variations in the slopes of species richness–climate relationships across both angiosperm and eudicot families (Table 2; Supplementary material Appendix 3–4 Table A3.4–A3.6, A4.3–A4.5, Fig. A3.12–A3.14, A4.9–A4.11). Diversification rate had significant but weak explanatory power for variations in the slopes of species richness–climate relationships, but family age had no significant effects.

Discussion

In this study, we investigated the effects of evolutionary processes on species richness–climate relationships for woody

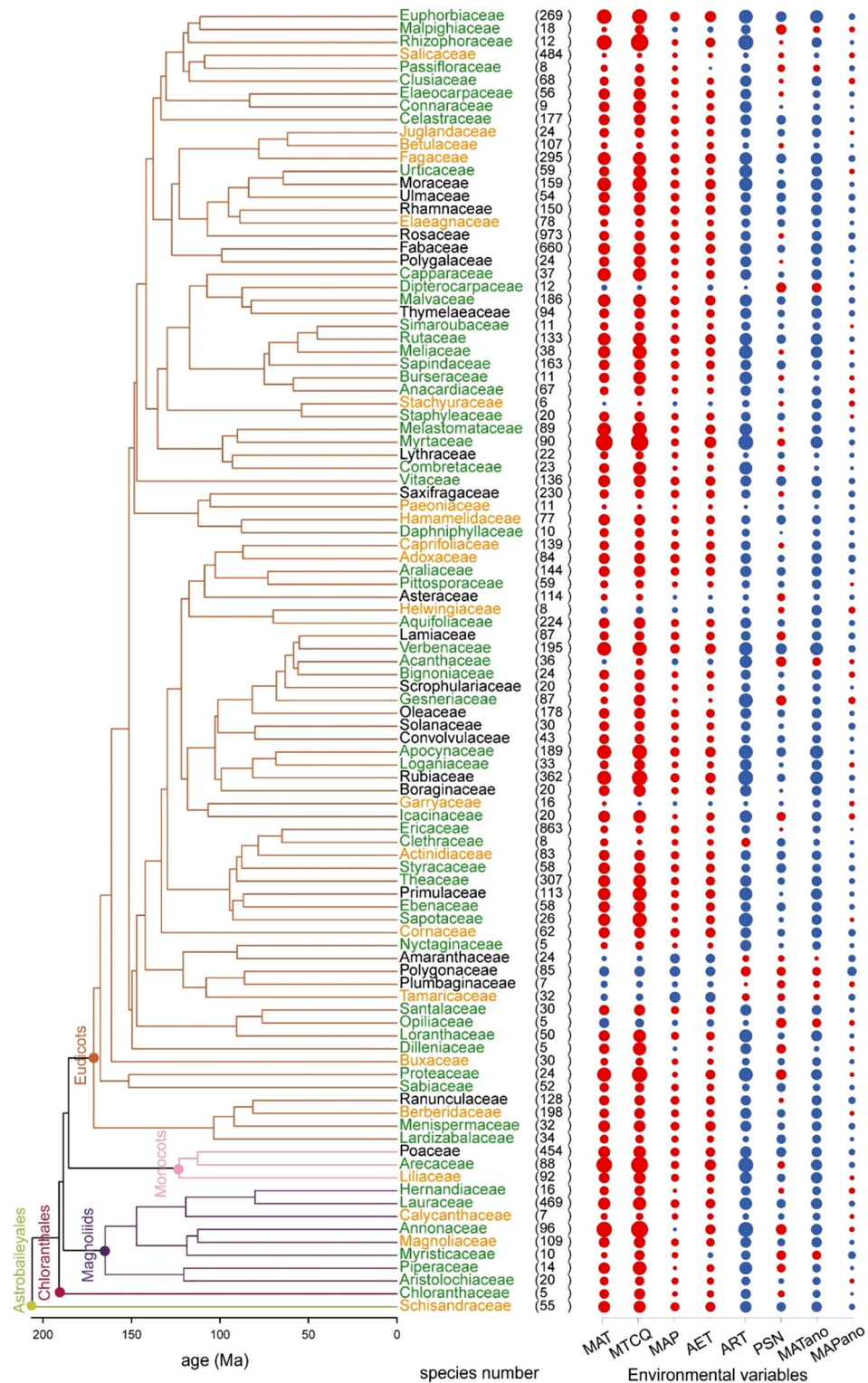


Figure 3. The slopes of relationships between family-level species richness and environmental factors shown on the phylogeny of Barba-Montoya et al. (2018). The dot size is proportional to the slopes. Red and blue dots show positive and negative relationships respectively. Families with tropical, temperate and cosmopolitan affinities are shown in green, orange and black colors respectively. The species number of each family found in eastern Eurasia is shown in parentheses.

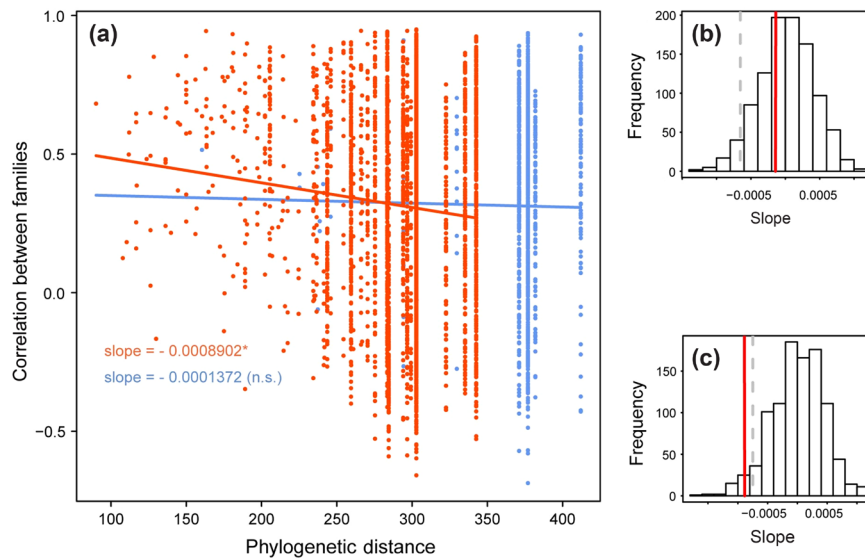


Figure 4. Relationships between correlations of family-level species richness and phylogenetic distance of corresponding family pairs (a) and the frequency distributions of slopes extracted from 1000 tip-swapped randomizations for angiosperms (b) and eudicots (c) based on the phylogeny of Barba-Montoya et al. (2018). In (a), orange symbols represent eudicots, while all dots and the blue line represent angiosperms. In (b) and (c), red lines represent the observed slopes and gray dash lines represent the 2.5% quantile of slopes from randomizations. Closely related families within eudicots have significantly more similar species richness patterns than distantly related families (Wilcoxon rank-sum test, $p < 0.05$).

plants in eastern Eurasia. We found that species richness–climate relationships were significantly phylogenetically conserved within both angiosperms and eudicots. We further found that the differences between ancestral and contemporary climatic niches of families were the dominant predictor of variation in the slopes of species richness–climate relationships, which suggests that niche conservatism may dominate species richness–climate relationships compared with diversification rate and time for speciation. It is noteworthy that the strength of phylogenetic niche conservatism might differ among different plant life forms (Qian et al. 2014, 2017), at different evolutionary depths/scales (Ricklefs and Renner 2012, Peixoto et al. 2017) and across different regions (Lu et al. 2018). Moreover, spatial scale (including extent and resolution) may also influence species richness–climate relationships (Rahbek and Graves 2001, Wang et al. 2012b). Therefore, the consistency of our findings with patterns at

a global scale, among different regions and between woody and herbaceous species remains to be tested using large-scale comprehensive distributional data with different resolutions. Nevertheless, eastern Eurasia has a large span of latitude and longitude from the tropics to the Arctic. Therefore, given the lack of comprehensive global distributional data and the paucity of information for herbaceous species, eastern Eurasia and particularly woody plants become a suitable choice for inferring the broad-scale species richness patterns and their drivers.

Phylogenetic conservatism in species richness patterns

The similarity between species richness patterns of each pair of families was negatively but not significantly correlated with the phylogenetic distance between corresponding family

Table 1. Blomberg's K for the slopes of species richness–climate relationships of angiosperm and eudicot families with at least 5 species evaluated using the phylogeny of Barba-Montoya et al. (2018). See Supplementary material Appendix 3–4 for results for families with at least 10 species and based on other phylogenies.

Climatic category	Climatic variables	Angiosperms		Eudicots	
		Blomberg's K	p-value	Blomberg's K	p-value
Environmental energy	MAT	0.687	0.154	0.738	0.178
	MTCQ	0.738	0.050	0.788	0.048
Water availability	MAP	0.781	0.037	0.894	0.013
	AET	0.724	0.066	0.794	0.047
Climate seasonality	ART	0.698	0.113	0.786	0.046
	PSN	0.600	0.702	0.656	0.713
Past climate change	MATano	0.619	0.543	0.692	0.430
	MAPano	0.582	0.821	0.657	0.691

Table 2. The coefficients (Coef.), R^2 , p values (p) and AIC of phylogenetic generalized linear square (PGLS) regressions evaluating the effects of the differences between contemporary and ancestral climatic niche, diversification rate with low exaction ($\epsilon=0$) (DivR) and family age on slopes of species richness–climate relationships for families with at least 5 species. Here ancestral climatic niche was reconstructed for the stem node. PGLS regressions were conducted using the phylogeny of Barba-Montoya et al. (2018).

Dependent variables	Independent variables	Angiosperms				Eudicotss			
		Coef.	R^2	p	AIC	Coef.	R^2	p	AIC
MAT slope	MAT diff	−0.0543	0.17	0.000	172	−0.0524	0.18	0.000	146
	DivR	6.3566	0.07	0.005	184	5.2495	0.06	0.027	158
	age	0.0021	0.01	0.330	190	0.0026	0.01	0.370	163
MTCQ slope	MTCQ diff	−0.0504	0.26	0.000	191	−0.0469	0.26	0.000	163
	DivR	7.9816	0.08	0.003	212	6.7944	0.07	0.015	181
	age	0.0017	0.00	0.571	219	0.0037	0.01	0.306	186
MAP slope	MAP diff	−0.0004	0.15	0.000	−9	−0.0004	0.15	0.000	−2
	DivR	2.9462	0.09	0.002	−2	2.8530	0.08	0.006	3
	age	−0.0007	0.00	0.530	7	−0.0003	0.00	0.855	11
AET slope	AET diff	−0.0008	0.18	0.000	43	−0.0008	0.18	0.000	41
	DivR	4.0374	0.10	0.001	50	3.6058	0.08	0.006	47
	age	−0.0001	0.00	0.937	60	0.0006	0.00	0.722	55
ART slope	ART diff	0.0050	0.28	0.000	146	0.0048	0.29	0.000	126
	DivR	−7.8021	0.13	0.000	165	−7.0135	0.13	0.000	143
	age	0.0004	0.00	0.859	179	−0.0001	0.00	0.960	154
PSN slope	PSN diff	0.0213	0.13	0.000	92	0.0202	0.13	0.001	75
	DivR	−0.8389	0.00	0.529	105	−0.5576	0.00	0.692	88
	age	0.0011	0.01	0.432	105	0.0015	0.01	0.390	87

pairs for angiosperms, but was significantly negatively correlated for eudicots (Fig. 4). The discrepancy in the results of angiosperms and eudicots might be partly due differences in phylogenetic conservatism in their climatic niches, and partly due to the different evolutionary histories of different angiosperm subclades. For example, Austrobaileyales, Chloranthales and magnoliids diverged at a very early phase during angiosperm evolution and went through more climatic perturbation compared to eudicots, which might influence the speciation, innovation and extinction of these clades (Friis et al. 2011, Li et al. 2019). Furthermore, Monocots have relatively few woody plant species and the strength of their niche conservatism might differ from that of eudicots (Qian et al. 2014, 2017), which might also influence the similarity in species richness patterns between Monocot and other angiosperm subclades.

Our results suggest that closely-related families have more similar species richness patterns than distantly-related families within eudicots. This conservatism may be linked to their tendencies to retain ancestral ecological niches (i.e. niche conservatism) (Wiens and Graham 2005). Niche conservatism may restrict clade dispersal (Wiens and Graham 2005) and confine them to their ancestral environments (Kozak and Wiens 2010a, 2012). Therefore, closely related clades tend to have similar climate requirements and hence likely remain in similar geographical regions, leading to stronger correlations between the species richness patterns of closely related clades. Previous studies have shown significant niche conservatism and its influences on species richness patterns for several groups. For example, Davis (2005) studied the evolution in climatic niches within *Marmota* and showed that closely-related species have similar climatic niches. Such tendency has also been shown for amphibians (Hof et al. 2010)

and mammals (Cooper et al. 2011). Species richness of a clade tends to be higher within environments that are more similar to its ancestral niche (Wiens and Donoghue 2004, Donoghue 2008). Together these findings suggest that niche conservatism may largely account for the increased similarity in species richness patterns of phylogenetically related clades within eudicots.

Phylogenetic conservatism in species richness–climate relationships

Our results indicate significant phylogenetic signals in the relationships between species richness patterns and climate, especially the climate variables representing winter temperature (i.e. MTCQ), and water availability (i.e. MAP), for both angiosperms and eudicots (Table 1). Moreover, we also demonstrated that the difference between contemporary and ancestral climatic niches of families had stronger influence on variations in the slopes of species richness–climate relationships than diversification rate and time for speciation. Therefore, clades inhabiting climates less similar to their ancestral climatic niches tend to have flatter species richness–climate relationships. These results suggest that niche conservatism may be the dominant driver of the variations of species richness–climate relationships among different angiosperm clades, which may subsequently lead to similar species richness patterns along the climatic gradients among closely related clades. These findings are consistent with previous findings for other groups. For example, Buckley et al. (2010) found that the slopes of species richness–climate relationships of mammalian clades have significant phylogenetic signals and the variations in these relationships are shaped by phylogenetic constraints

and clade origins. Similarly, Economo et al. (2019) also found that phylogenetic niche conservatism alone is sufficient to produce the species richness patterns of *Pheidole*, a clade of ants with a Neotropical ancestor.

Winter coldness was one of the strongest predictors of species richness within tropical families (Fig. 2a, d) and the slopes of the relationships between species richness and winter coldness were significantly phylogenetically conserved for eudicots and marginally significantly conserved for angiosperms (Blomberg's $K=0.738$, $p<0.1$ for angiosperms and Blomberg's $K=0.788$, $p<0.05$ for eudicots; Table 1). This suggests that the effect of winter coldness on species richness is important both within and across families. In contrast, MAP did not substantially influence the species richness within most families (Fig. 2) but the slopes of species richness–MAP relationships exhibited the strongest phylogenetic signal among all richness–climate relationships (Blomberg's $K=0.781$ for angiosperms and Blomberg's $K=0.894$ for eudicots; $p<0.05$; Table 1). This may suggest an important partitioning of water sensitivity among and within families. Disentangling the mechanisms behind these variations was beyond the scope of the present study, but could provide exciting avenue for future research.

Our study indicates that species richness patterns of families with the same affinity are dominated by similar environmental factors (Fig. 2), which may reflect the effect of phylogenetic niche conservatism. We found that winter coldness is the best predictor for species richness of most tropical families. This might reflect the tendency of tropical clades to retain their ancestral climatic niche. Because tropical clades might have originated in warm climates, their dispersal into temperate climates is strongly limited by winter coldness due to niche conservatism (Latham and Ricklefs 1993a, Wiens and Donoghue 2004). Consistent with our findings, Wang et al. (2011) found that winter coldness constrained the species richness patterns of woody plants in China, especially for species with tropical affinity. Similarly, Giehl and Jarenkow (2012) demonstrated that tree species with tropical origin were generally more restricted to tropical sites than species with subtropical origins. Winter coldness, therefore, might have played an important role in preventing many tropical lineages from colonizing temperate latitudes, causing an uneven accumulation of species in the tropics and temperate regions.

The strong effects of winter coldness on species richness of tropical families and the conservatism in richness–winter coldness relationships may be linked to the morphological and physiological adaptations of plants to cold climate. These adaptive traits, which have strong heritable component, enable plants to survive in particular environments thereby influencing their richness–climate relationships. The adjustment in cell membrane properties and cell sap constituents, phenology controls (Körner et al. 2016) and adjustment in plant stature (Squeo et al. 1991) are some of the physiological and morphological adaptations of plants to cold climate with strong heritability. Ancestrally tropical plant lineages rarely

succeed in making a transition from tropics to temperate (Donoghue 2008) due to difficulty in evolving such adaptive traits. The distributions of tropical clades are therefore always strongly influenced by cold winter temperature.

In contrast to the tropical families, species richness of families with temperate affinity is high in subtropical mountains, as well as temperate and boreal regions. Winter coldness is not the primary limitation for the richness of these species, while Quaternary climate change becomes an important factor. This variation in the species richness–climate relationships between families of tropical and temperate affinities suggests that these relationships might be rooted in the evolutionary history of these clades.

Effects of Quaternary climate change on woody plant species richness in eastern Eurasia

Our results suggest that climate change since the LGM dominated species richness patterns of most temperate families in eastern Eurasia (Fig. 2). Moreover, the average explanatory power of temperature anomaly was comparable to that of winter coldness for temperate families. These results are in contrast to previous studies indicating that Quaternary climate change has weak effects on species richness patterns in eastern Asia (Qian and Ricklefs 1999, 2000, López-Pujol and Ren 2010). This inconsistency might be because most previous studies in eastern Asia did not separately evaluate the effect of past climate change on species with different affinities (e.g. tropical- versus temperate-affinity). Because of the dominance of tropical families, the effects of past climate change may have been masked when evaluated for tropical and temperate species combined. Similar to our findings, previous studies conducted in other regions mainly focusing on species richness of temperate clades in high latitudes (e.g. tree species richness in Europe (Svenning and Skov 2007), Holarctic trees in Europe and North America (Montoya et al. 2007), reptiles and amphibians in Europe (Araújo et al. 2008), etc.) normally identified Quaternary climate change as a strong determinant of species richness patterns. Together these findings suggest that, while the influence of Quaternary climate change might appear to be less important for overall species richness, the influence tends to be stronger on species richness patterns for temperate than for tropical clades.

Why are temperate clades strongly influenced by past climate change? The southern part of eastern Eurasia was far away from glaciers and was only mildly affected by glaciation during the LGM (Qian and Ricklefs 1999, 2000), while the temperate and boreal regions, where many temperate clades (e.g. Cyperaceae, *Quercus* s.s., Ericaceae) are thought to have originated (Manos et al. 1999, Escudero et al. 2012, Hou et al. 2016), were more severely influenced by glaciers during the LGM (Sandel et al. 2011). It is likely that some temperate species in the northern part of eastern Eurasia might have retracted southward to survive severe climate changes (Qian and Ricklefs 2000) and after the glacial periods, they might have migrated back towards the north (Svenning et al.

2008b) or to mountain tops in the subtropical and temperate regions (Qian and Ricklefs 2000).

Conclusions

Here, we found phylogenetic signals in species richness patterns for eudicot families and in the slopes of species richness–climate relationships for all angiosperm families, suggesting that both species richness patterns and species richness–climate relationships may be evolutionarily conserved at certain phylogenetic levels. We further demonstrated that the difference between contemporary and ancestral climatic niches dominated the variations in the slopes of species richness–climate relationships. We also showed that Quaternary climate change had strong impacts on species richness patterns of temperate families, but not tropical families. Overall our findings suggest that niche conservatism is the dominant factor for the evolution of, and variations among, species richness–climate relationships, and that phylogenetic conservatism might be one of the major mechanisms underlying the broad-scale species richness patterns.

Data availability statement

The distribution of species richness of each family and the climate data in each grid cell in eastern Eurasia are available in Dryad Digital Repository (<https://doi.org/10.5061/dryad.nk98sf7qh>) (Su et al. 2020). Species distribution maps are available upon request.

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Author contributions – ZW, XS and XX conceived the idea and designed the study; ZW, XS, XX, DS and SW collected the data; XS, ZW analyzed the data; XS, ZW and NS led the writing, and all authors contributed substantially to revisions and approved the submission.

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Supplementary material (available online as Appendix ecog-04839 at <www.ecography.org/appendix/ecog-04839>). Appendix 1–4.